SOLITARY WASPS FROM SUBARCTIC NORTH AMERICA – II. SPHECIDAE FROM THE YUKON AND NORTHWEST TERRITORIES, CANADA: DISTRIBUTION AND ECOLOGY

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Sphecid wasps of 35 species were collected in the Yukon and Northwest Territories during the summers of 1967 and 1968. Literature about these species is reviewed. Latitude, vegetation, soil type and slope of the study areas are analyzed as is their use by the wasps, for feeding, preying, nesting and basking. Particularly well represented in these samples are the subfamilies Crabroninae and Pemphredoninae, and the genera Ammophila, Podalonia *and* Tachysphex. *Included are circumpolar, Holarctic and Nearctic species. Some of the last-named group range widely, with populations occurring as far south as Florida and Mexico.*

Trente-cinq espèces de sphégides ont été récoltées au Yukon et dans les Territoires du Nord-Ouest au cours des étés 1967 et 1968. Le texte comprend un compte-rendu de la bibliographie relative à ces espèces. On y trouvera une analyse de la latitude, de la végétation, de la nature du sol, de la pente des régions étudiées ainsi que de l'utilisation qu'en font les sphégides en fonction de leur comportement alimentaire et nidificateur, de la sélection des proies et de leur exposition au soleil. Ce sont surtout les sous-familles Crabroninae et Pemphredoninae et les genres Ammophila, Podalonia *et* Tachysphex *qui sont bien représentés parmi cette faune. On y trouve aussi des espèces circumpolaires, holarctiques et néarctiques. Pour le dernier groupe nommé, la distribution est très large, avec des populations pouvant atteindre des régions aussi méridionales que la Floride et le Mexique.*

Despite severe climatic conditions and a short season favorable for activity, many species of the family Pompilidae are represented in the subarctic regions of North America (Steiner, 1970). This paper deals with another family of solitary wasps, the Sphecidae, having representatives which were collected in the same study area.

This paper describes habitats and microhabitats, and provides data about the uses made of these by different species of sphecids. These wasps are much more diversified in their ecological and behavioral characteristics than are pompilids. Sphecids are well suited for behavior-ecology studies, particularly for those concerning adaptations for avoiding competition at the community level.

THE STUDY AREAS

General features and maps of the regions visited and of the localities sampled have been previously presented (Steiner, 1970). Additional data are provided in Table 1.

Climax communities of the boreal forest and taiga do not appear to provide particularly favorable habitats for solitary wasps but some natural or man-disturbed areas in the north are potentially good habitats. These include pits, river banks, lake shores, flats, outwash plains and forest edges. Most of the sphecids discussed were collected in such places. Figures 1 to 9 illustrate five locality types from which samples were collected.

Table 1. Distribution per species and localities.

Species	Localities (and latitude N.)	N. W. T.														Y. T.										Total number of localities where species found
	I. Ft. Smith (59° 58')	II. Sass River (60° 10')	III. Wood Buffalo (60° 28')	IV. Enterprise (60° 40')	V. Buffalo River (60° 45')	VI. Hay River (60° 45')	VII. Heart Lake (60° 50')	VIII. Kakisa River (61°)	IX. Ft. Providence S. (61° 17')	X. Ft. Providence N. (61° 17')	XI. Birch Lake (62°)	XII. Yellowknife (62° 27')	XIII. Prelude Lake (62° 32')	XIV. Frank Channel (62° 43')	XV. Rae (62° 46')	A. Marsh Lake (60° 30')	B. Pikhandle Lake (61° 57')	C. Tatchun Lake (62° 20')	D. Minto (62° 37')	E. Stewart River (63° 26')	F. Taylor Creek (63° 30')	G. Mayo (63° 38')	H. Gravel Lake (63° 47')	I. Keno Hill (63° 54')	J. Dawson City (64° 10')	
1. *Diploplectron peglowi*										+			+													2
2. *Astata nubecula*								+			+		+	+												4
3. *Dryudella picta*										+			+													2
4. *Miscophus americanus*											+															1
5. *Tachysphex aethiops*						+				+		+	+	+												5
6. *T. quebecensis*										+		+		+												3
7. *T. terminatus*													+	+												2
8. *Diodontus* sp.			+			+																				2
9. *Mimesa pauper*										+		+	+	+												4
10. *Mimumesa clypeata*									+	+																2
11. *M.* sp.										+		+		+												3
12. *Pemphredon bipartior*													+													1
13. *P. montana*							+																			1
14. *Ammophila azteca*			+		+	+	+		+	+	+	+	+	+	+		+			+		+				14

15. *A. mediata*	+			+					+				+	+			+	+							7
16. *A. strenua*									+																1
17. *Podalonia luctuosa*		+																							1
18. *P. robusta*						+			+	+		+		+			+								6
19. *Alysson triangulifer*									+																1
20. *Nysson lateralis*							+			+	+		+												4
21. *N. subtilis*									+		+														2
22. *Lestiphorus cockerelli*									+																1
23. *Gorytes albosignatus*									+																1
24. *Cerceris nigrescens n.*	+						+		+	+	+	+	+	+					+						9
25. *Crabro latipes*						+	+		+	+	+	+	+	+							+				8
26. *C.* sp.													+												1
27. *Crossocerus* sp.									+	+				+											3
28. *Ectemnius arcuatus*										+															1
29. *E. dives*										+															1
30. *E. lapidarius*																					+				1
31. *E. nigrifrons*		+			+				+	+			+					+		+	+				8
32. *E. trifasciatus*			+							+				+											3
33. *E.* sp.										+															1
34. *Lestica producticollis*										+															1
35. *Oxybelus uniglumis 4-notatus*					+					+	+			+											4
Total number species per sampling locality	2	2	3	1	3	5	5	1	7	25	8	8	14	14	1		3	2		3	4				
Intensity of sampling	–	–	–		–			–		*				*		–			–			–	–	–	

* localities intensively sampled.
– localities sampled very incompletely and superficially.

In the Northwest Territories study area, most localities are on plains and plateaus to the west of the Canadian Shield. However, localities XII, XIII and XV are on the Canadian Shield and locality I (Fort Smith) is near its western edge. In this area samples were collected throughout the summers of 1967 and 1968. The Yukon study area was visited only briefly after mid-August of 1968. Locality X (Fort Providence, in the Mackenzie River valley, Fig. 1 and 2) was the most favorable area visited and was the most intensively investigated.

Eleven habitats are recognized. They are characterized below in terms of slope, vegetation and soil. Also described are the uses made of each habitat by its sphecid inhabitants. See Table 2 for an explanation of letters in Figures 1 to 9.

Table 2. Explanation of letters in Figures 1 to 9. (Typical wasp habitat facies and microhabitats in some Northwest Territories sample localities)

a = Immature aspen interspersed with willow and shrub
b = Low spoilbank (small man-made ridge)
c = Flat area, covered with dense, low vegetation
d = Patches of *Achillea millefolium* (yarrow)
e = Flat area, sparsely vegetated
f = Patches of *Epilobium* species (fireweed)
g = Spruce/Jackpine forest (interspersed with aspen)
h = Collapsed cutbanks (steep slope)
i = Patches of shrubby vegetation (*Rosa* sp., *Salix* sp., *Betula* sp., *Alnus* sp., etc.)
j = Edge of mature forest (with shrub understory)
k = Decaying exposed tree roots and branches
l = Decaying, partially buried logs
m = Spruce forest
n = Tall grasses
o = Vegetated spoilbank (gentle slope)
p = Vegetated ditchside
q = Non-vegetated man-made disturbed area
r = Edge of mature forest
s = Hummocky, richly vegetated area
t = Poorly drained flat bottom of shallow borrow pit
u = Elevated area left around base of large tree
v = Tension zone (ecotone); transition zone from bog to upland (dense low shrubby vegetation)
w = Cutbank of borrow pits resulting from excavation
x = Spoilbank in the process of becoming vegetated
y = Flat vegetated flood plain of river

1). *Recently disturbed, flat, unvegetated areas with friable (often sandy) soil* (*q*, Fig. 5 and 7). – These areas border the highway in dugouts, borrow pits, sand and gravel pits (Fig. 5), or border lake shores (Fig. 7) and river banks and were in localities I, VI, VII, XI, XII, XIII and XIV.

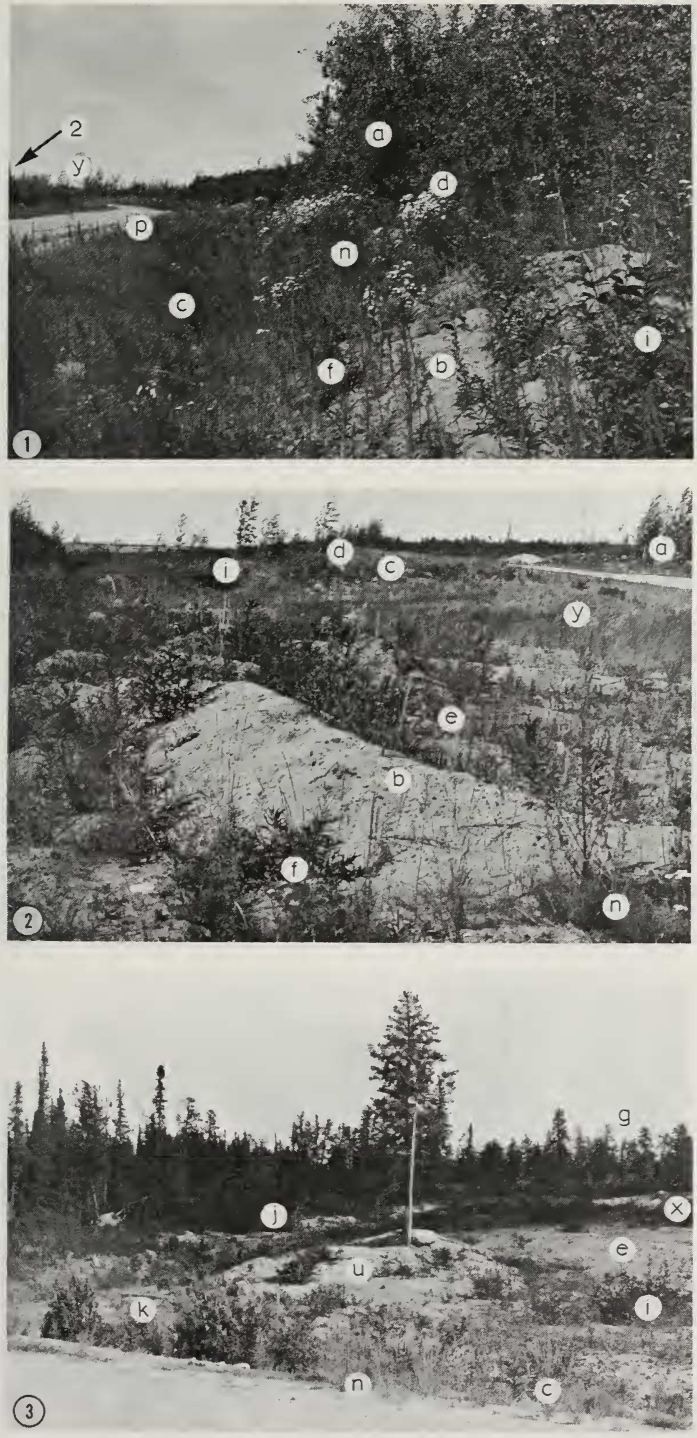

Fig. 1-2. Flood plain of Mackenzie River with flat, low vegetated areas (Fig. 2) and juxtaposition of spoilbanks and forest edge habitats, of sandy soil (Fig. 1). (Ft. Providence: X, 9 August 1967). Fig. 3. Shallow borrow pit along highway, in the process of becoming vegetated; friable soil. (Frank Channel: XIV, 8 August 1967)

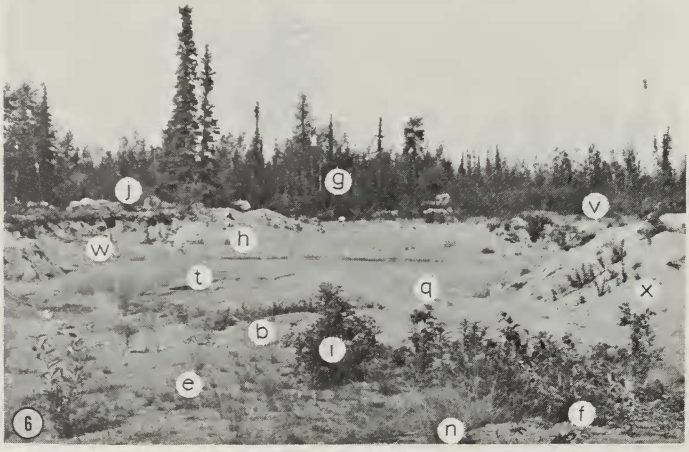

Fig. 4-5. Man-made gravel/sand pit, along highway, with friable soil: general view (Fig. 5) and detail of gently sloping area (Fig. 4) with various microhabitats. (Birch Lake: XI, 2 August 1967). Fig. 6. Deep borrow pit in compact, poorly drained soil, with tension zone between bog and upland. (Rae: XV, 8 August 1967)

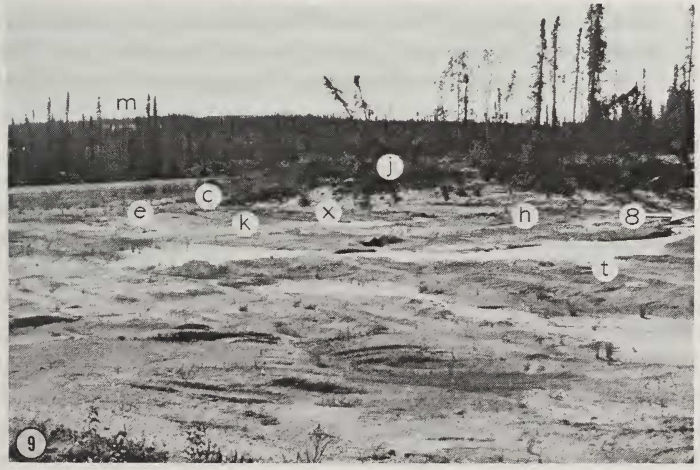

Fig. 7-9. Disturbed areas on sandy lake shore areas (Fig. 7-8) near forest edges, and extensive man-made bare and poorly drained area, along the highway (Fig. 9). (Prelude Lake: XIII, 7 August 1967)

If it is situated adjacent to a vegetated area this habitat is used occasionally by wasps for basking early in the morning. Those most frequently observed were members of *Astata nubecula*, members of the genera *Ammophila, Podalonia* and *Tachysphex* and a few pompilids and crabronines. A few females of *Tachysphex terminatus* were seen digging in such areas, but usually in sparsely vegetated areas.

2). *Recently disturbed, sloping, unvegetated areas of friable soil* (*h*, Fig. 5 and 9). – These often consist of steep (*h*, Fig. 5) or gently sloping, man-made, collapsed cutbanks and spoilbanks and were found in localities I, VII, XI (Fig. 5, *h*), XII, and XIII (Fig. 9, *h*).

Such areas resemble habitat type 1 but, when favorably exposed to the morning sun, are used more consistently by wasps for basking. Males of *Astata nubecula* were at site *h* (Fig. 5) perched on prominent features of the landscape such as boulders and stumps that were also used as observation posts. Specimens representing the other taxa listed for habitat 1 were found in habitat 2, also.

3). *Man-made, poorly-drained, flat bottoms of borrow pits, usually in compact soil* (*t*, Fig. 6 and 9). – This habitat was extensive in locality XIII (*t*, Fig. 9), less so in locality XV (*t*, Fig. 6).

A relatively large amount of soil moisture rendered this type of habitat generally unsuitable for wasps, although a few females of *Ammophila* and *Podalonia* carried prey across such areas. Drier sections of this habitat were used for nesting by a few females of some species, such as *Cerceris nigrescens* (XV, Fig. 6), which usually nest in habitats with more friable soil (XI, Fig. 4 and 5).

4). *Flat or gently sloping, sparsely-vegetated areas* (*e* in most Figures, *y* in Fig. 2). – Usually of friable soil, these areas are: (a) man-made, occurring in pits (Fig. 4 and 5); or (b) natural, on flood plains of rivers (*y*, Fig. 2) and lake shores. They were extensively represented in most localities, particularly along flood plains of the Mackenzie (IX and X) and of the Hay Rivers (VI), and shores of Great Slave Lake (XIV) and Prelude Lake (XIII).

These areas were used extensively as nesting grounds by females of *Ammophila, Podalonia, Tachysphex* (particularly *T. aethiops*, the most common species of this genus), *Nysson*, *Cerceris* and some Crabroninae. A few nests of *Oxybelus* were seen here, but they were more common on more sloping ground. Females of small species of Pemphredoninae and Crabroninae, which prey on small insects, used these areas mainly for hunting and less frequently for basking and feeding. Females of the larger wasp species hunted mainly in more densely vegetated areas, which had a more abundant flora and insect fauna.

5). *Flat areas, densely covered with herbaceous vegetation* (*c* in most Figures). – Most localities included this type of habitat, but it was best developed along the Mackenzie River (X, Fig. 1 and 2).

An abundant and diverse insect fauna was found in these areas, including acridoid grasshoppers, leafhoppers, small beetles, many flies, bugs, lepidopterous caterpillars, and representatives of other groups. Most flowers on which the sphecid wasps fed occurred in these areas.

Although many wasps hunted and fed in this type of habitat, nests were rare. Sphecids of the genus *Tachysphex* and pompilids used this habitat most intensively as hunting ground. Females of *Tachysphex* prey mainly on the immature acridids and tetrigids, abundant in these places. Other hunters observed were females of *Ammophila* and *Podalonia* species.

Patches of fireweed (*Epilobium*, *f*, Fig. 1, 2, 4 and 8), yarrow (*Achillea millefolium*, *d*, Fig. 1 and 2), and undetermined umbellifers, common in this habitat, were intensively exploited as a source of food by wasps of many species, particularly in the morning.

6). *Low spoilbanks and man-made ridges of friable soil in the process of becoming vegetated* (*b*, Fig. 1 and 2; *o*, Fig. 4; *x*, Fig. 5, 6 and 9). – This type of habitat provides nesting

grounds for many species. Along the Mackenzie River (X, Fig. 1 and 2) these areas were used as nesting grounds by females of *Oxybelus uniglumis quadrinotatus, Mimesa pauper, Mimesa clypeata, Dryudella picta* and *Diploplectron peglowi. Dryudella* males exhibited territorial behavior, as described for *Astata nubecula* (Evans, 1970: 487-488). The only specimens of *Miscophus americanus* from the study areas were found in a similar habitat (locality XI).

These areas were used extensively by female insects which prey on sphecids: the inquilinous sphecids of the genus *Nysson*; chrysidid wasps; and parasitoid Diptera. Other sphecids did not extensively use these areas as hunting grounds.

Patches of yarrow (*d*, Fig. 1) and fireweed (*f*, Fig. 2) growing in these areas were exploited for food by many wasps. Basking was observed on the spoilbanks. On spoilbanks situated adjacent to shrubby and sparsely-forested habitats (*a*, Fig. 1), interactions between and within species were most intense, frequent and complex due to the addition of Pemphredoninae and Crabroninae, characteristic of shrubby habitats.

7). *Shrubby, brushy and sparsely-forested areas, with understory* (*a, i, j, r, s, v,* Fig. 1-9). – Such habitat includes stands of aspen interspersed with willow and shrub (*a*, Fig. 1), edges of mature forest with shrub understory (*j*, Fig. 3, 5 and 9; *r*, Fig. 7) and ecotones (tension zones) such as those between bog and upland, having dense, low, shrubby vegetation (*v*, Fig. 6).

These areas provide both nesting and hunting sites for those pemphredonines and crabronines that are twig nesters, such as *Mimesa* sp. and *Pemphredon bipartior* for the former, *Ectemnius* for the latter. But they provide only hunting sites for those crabronines that are ground nesters, such as *Crabro latipes*. An occasional nest of *Tachysphex aethiops* and of *Podalonia robusta* was found on the ground, but only in thinly-vegetated areas or at the edges of this habitat type. Females of *Crabro latipes* and *Ectemnius nigrifrons* hunted in the leaves of shrubs. Females of the philanthine *Cerceris nigrescens nigrescens*, which prey on small weevils (Evans, 1970: 501; Muesebeck et al., 1951: 1009; Scullen and Wold, 1969: 212), used extensively as hunting grounds area *v* (Fig. 6).

Males of crabronines, especially *C. latipes*, were numerous and were probably attracted by the hunting females. They attempted to mate with females and with other males particularly at sites *a* (Fig. 1) and *j* (Fig. 9). Males of some undetermined pemphredonines behaved similarly. A few males of the larrine *Tachysphex aethiops* were also found in such a habitat, investigating the leaves of a small *Alnus* bush. They were perhaps feeding, as individuals of several other species of Larrinae are known to lick exudations of sap from various plants or shrubs.

Between bouts of hunting, the occasional crabronine basked in this habitat, flattening itself on an exposed leaf or against a tree trunk. Early in the morning, however, they basked mainly on boulders or on the ground in non-vegetated or sparsely-vegetated areas adjacent to the brushy hunting grounds.

8.) *Patches of shrubby vegetation (including populations of* Rosa, Salix, Betula *and* Alnus*)* (*i*, Fig. 4 and 5) *or hummocky, richly-vegetated areas* (*s*, Fig. 8). – These areas provide suitable situations for the twig-nesting species. They were also visited by ground-nesting crabronines and pemphredonines during their hunting trips. The few specimens seen or captured of *Lestiphorus cockerelli, Gorytes albosignatus* and *Alysson triangulifer* were found in this habitat. From circumstantial evidence, I think the latter were hunting, not nesting, here. One individual of *G. albosignatus* was found digging the soil in a different habitat (site *b*, Fig. 2), and insofar as is known Nearctic *Alysson* females nest in the soil (Muesebeck et al., 1951: 980).

9). *Decaying, often partially buried logs* (*l*, Fig. 4) *and decaying exposed tree roots and branches* (*k*, Fig. 5 and 8). – These sites were visited by pemphredonines and crabronines some of which inspected abandoned galleries of wood borers (hunting or nest-seeking behavior?). Female crabronines of *Ectemnius arcuatus* and *E. dives* are known to nest in logs, timber and stems (Muesebeck et al., 1951: 1026-1027). A few wasps (pemphredonines, crabronines, *Ammophila azteca* and others) basked in these places, and males of *Astata nubecula* used them for observation posts.

10). *Vertical banks (sand cliffs; cutbanks; river cutbanks; cutbanks of borrow pits)* (*w*, Fig. 6). – In locality VI, females of the small pemphredonine *Diodontus* were found inspecting, both in flight and by walking, such cutbanks and the burrows therein, possibly for prey or for nesting sites. Other wasps found here consistently were: a small crabronine, undetermined, possibly a member of the genus *Crossocerus*; some vespids; and some chrysidids. Occasional basking was also observed here.

11). *Dense, spruce-jackpine* (*g*, Fig. 3, 5, 6, 7 and 8) *and spruce stands* (*m*, Fig. 4 and 9). – These areas were seldom visited by wasps.

Discussion. – When nesting, hunting, feeding and basking sites were close together, as in locality X (Fig. 1), conditions appeared particularly favorable for many wasps. Indeed, the speed with which prey capture and nest provisioning can be completed may be crucial, particularly in northern climates where favorable weather is limited (Evans, 1970).

Considerable segregation in habitat and microhabitat was noticed among sphecid wasps, much more so than among the spider wasps studied previously (Steiner, 1970). Competition among species is thus considerably reduced, and is further reduced by behavioral specialization in prey selection and hunting techniques (Evans, 1970). Further segregation is achieved by some stratification of the nest cells in the soil, at different depths according to species (Evans, 1970). However, there was little species segregation at feeding and at basking sites.

ANNOTATED LIST OF SPECIES

Family Sphecidae
Subfamily Astatinae
Genus *Diploplectron* Fox

Known biology. – Females nest in open sandy places (Evans, 1957: 180). Prey consists of adults or nymphs of Hemiptera. Williams (1946: 648) provides details.

Known distribution. – North America and South Africa (Evans, 1957: 180).

1. *Diploplectron peglowi* Krombein.

Known distribution. – New York: Oswego Co. (Muesebeck et al., 1951: 939).

Author's records. – NORTHWEST TERRITORIES. – X, ♂, 2 ♀♀ 31 July 1967. XIII, 2 ♂♂, ♀ 6 August 1967 (♀ hunting); ♂ 7 August 1967.

Genus *Astata* Latreille

Known biology. – Females of this genus provision their nests with Hemiptera, especially pentatomids and lygaeids (Muesebeck et al., 1951: 939).

2. *Astata nubecula* Cresson.

Known biology. – Females nest in bare, hard, stony soil, and provision their nests with immature stink bugs (*Chlorochroa uhleri* Ståhl) carried in flight (Evans, 1970). Nymphs

of *Thyanta* have also been recorded as prey (Krombein et al., 1967: 387). Males exhibit territorial behavior (Evans, 1970).

Known distribution. – Western United States, Oregon to New Mexico north to Idaho (Muesebeck et al., 1951: 940). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 129).

Author's records. – NORTHWEST TERRITORIES. – VIII, ♂ 10 August 1967 (returns and lands on exactly the same spot); ♀ 2 August 1967 (exploring). XIII, 3 ♂♂ 30 July 1968 (each lands on conspicuous, elevated objects such as stumps, fallen logs and rocks); 2 ♂♂, ♀ 7 August 1967. XIV, ♂ 8 August 1967 (returns and lands on same spot).

Genus *Dryudella* Spinola

3. *Dryudella picta* (Kohl).

Author's records. – NORTHWEST TERRITORIES. – X, ♂, ♀ 17 July 1968 (*in copula*, the male carrying the female under him in flight in prey-like fashion, and landing from time to time); ♂ 21 July 1967 (basking in the morning sun). XIII, 2 ♂♂ 7 August 1967 (returning to and landing on same spots, repeatedly).

Subfamily Larrinae
Tribe Miscophini
Genus *Miscophus* Jurine

Known biology. – Females nest in sandy soil and provision their nest cells with tiny spiders transported in a series of low flights (Kurczewski, 1969).

4. *Miscophus americanus* (W. Fox).

Known biology. – Kurczewski (1969) presented a detailed study of the biology of this species. Notes were published by Hartman (1905: 69-70), and Krombein (1952b: 328). Adults are found on sand, on bare places and in woods. Females nest in well-packed sand in slightly sloping areas. Prey consists of immature spiders of the families Epeiridae (Hartman, 1905) and Theridiidae (Kurczewski, 1969). The latter author provides data on prey hunting behavior, nest provisioning, nest structure, and position of the egg on the prey.

Known distribution. – Eastern North America, from New York south to Florida and west to Colorado (Muesebeck et al., 1951: 944) and Alberta (Strickland, 1947: 129).

Author's records. – NORTHWEST TERRITORIES. – XI, 2 ♂♂ 2 August 1967.

Tribe Tachytini
Genus *Tachysphex* Kohl

Known biology. – Prey species are orthopteroids, mostly immature acridids, but females of some species also capture mantids and blattids (Muesebeck et al., 1951: 950).

5. *Tachysphex aethiops* (Cresson).

Known biology. – A nest was found on flat, friable sand 2 meters from a river bank. The prey therein was an immature acridid grasshopper of the genus *Trimerotropis* (Evans, 1970: 489-490).

Known distribution. – Western United States in mountains (Muesebeck et al., 1951: 950). Wyoming: Jackson Hole (Evans, 1970).

Author's records. – NORTHWEST TERRITORIES. – VI, ♂, ♀ 29 July 1967; ♂ 12

August 1967. X, ♀ 11 August 1968 (apparently hunting); ♀ 25 August 1967. XII, 3 ♀♀ 29 July 1968 (hunting and nest digging in sandy hillocks). XIII, 2 ♂♂, 2 ♀♀ (former investigating leaves of small *Alnus* bush) 30 July 1968; ♀ 6 August 1967. XIV, 2 ♂♂ 8 August 1967.

6. *Tachysphex quebecensis* Provancher.

Known biology. – Prey: immature acridids of the genera *Camnula* and *Melanoplus* (Krombein et al., 1967: 393).

Known distribution. – Transcontinental in northern United States and southern Canada, Quebec to California, in north (Krombein et al., 1967: 393; Muesebeck et al., 1951: 952).

Author's records. – NORTHWEST TERRITORIES. – X, ♂ 25 July 1967; ♀ 26 July 1967. XII, ♀ 29 July 1968. XIV, ♂, ♀ 26 July 1968.

7. *Tachysphex terminatus* (F. Smith)

Known biology. – Adults are found in woods and in barrens (Krombein et al., 1952b: 330). Nests are in open places, in sand or in loose topsoil (Krombein et al., 1958: 188; Muesebeck et al., 1951: 953). Prey includes tetrigids and immature acridids of many genera (Muesebeck et al., 1951: 953). The latter group includes *Melanoplus* and *Tryxalus* (Krombein et al., 1958: 188; Kurczewski, 1966a), and *Chorthippus curtipennis* (Harris) (Evans, 1970: 491). Female closes entrance while away from burrow (Evans, 1970). Male behavior was studied by Kurczewski (1966b). Data about population ecology of this species are recorded by Kurczewski and Harris (1968).

Known distribution. – Transcontinental, in the north from Quebec to British Columbia; southward in the east to Georgia and westward to Arizona (Krombein et al., 1967: 393; Muesebeck et al., 1951: 953). Alberta (Strickland, 1947: 129).

Author's records. – NORTHWEST TERRITORIES. – XIII, ♀ 30 July 1968 (starting nest digging in the ground). XIV, 2 ♂♂ 8 August 1967.

Subfamily Pemphredoninae
Tribe Psenini
Genus *Diodontus* Curtis

Known biology. – Nests are in cavities in logs, or stems of plants, such as canes of *Rubus* (Muesebeck et al., 1951: 958; Spooner, 1948: 129-172). Females of Palaearctic species prey on aphids and psyllids, which are carried ventrally by the middle legs (Spooner, 1948). Prey records are not available for the Nearctic species.

8. *Diodontus* sp. (or spp.?).

Author's records. – NORTHWEST TERRITORIES. – III, ♀ 14 August 1967. VI, 3 ♂♂, 2 ♀♀, 29 July 1967 (investigating vertical cutbanks); ♂, ♀ 12 August 1967.

Genus *Mimesa* Shuckard
Subgenus *Mimesa* (*sensu stricto*)

Known biology. – Females nest in soil. Prey consists of cicadellids, which the female carries with her middle legs (Muesebeck et al., 1951: 958; Spooner, 1948).

9. *Mimesa pauper* Packard.

Known biology. – Adults at edge of woods on high foliage (Kurczewski and Kurczew-

ski, 1963:146).

Known distribution. – Transition zone east of Rocky Mountains (Muesebeck et al., 1951: 960).

Author's records. – NORTHWEST TERRITORIES. – X, ♀ 11 July 1968 (investigating insect burrows, holes, in the soil); 3 ♀♀ 31 July 1967 (same remark). XII, one (sex?) 29 July 1968 (same remark). XIII, 4 ♂♂ (on leaves of small trees) 7 August 1967. XIV, ♂ 26 July 1968; 4 ♀♀ 8 August 1967.

Subgenus *Mimumesa* Malloch

Known biology. – Females of Palaearctic species nest in cavities in logs and stems. Their prey consists of delphacids and cicadellids, which the female wasp carries in her mandibles (Spooner, 1948). Data about biology are not available for Nearctic species.

10. *Mimesa clypeata* (W. Fox).

Known distribution. – Western North America: California and Nevada north to Alaska (Muesebeck et al., 1951: 961).

Author's records. – NORTHWEST TERRITORIES. – IX, ♀ 1 August 1967 (investigating the ground, holes, burrows). X, ♀ 26 July 1967.

11. *Mimesa* species.

Author's records. – NORTHWEST TERRITORIES. – X, ♀ 22 July 1967 (flying around shrubs). XII, ♂ 4 August 1967. XIV, 2♀♀ 8 August 1967 (flying around young aspen and big boulders).

Tribe Pemphredonini
Genus *Pemphredon* Latreille

Known biology. – Females nest in twigs, deserted galls, abandoned beetle burrows, or in rotten wood, and provision the cells with bugs of the family Aphidae (Muesebeck et al., 1951: 965).

12. *Pemphredon bipartior* W. Fox.

Known biology. – Nests in twigs of sumac and elder. Prey: ?*Eriosoma lanigerum* (Hausmann); *Rhopalosiphum rhois* Monell (Muesebeck et al., 1951: 966).

Known distribution. – Eastern United States, New York to Texas (Muesebeck et al., 1951: 966).

Author's records. – NORTHWEST TERRITORIES. – XIII, 2 ♂♂ 7 August 1967.

13. *Pemphredon montana* Dahlbom.

Known distribution. – Holarctic. Nearctic Region: British Columbia. Palaearctic Region: Europe (Muesebeck et al., 1951: 965).

Author's records. – NORTHWEST TERRITORIES. – VII, ♀ mid-July 1968.

Subfamily Sphecinae
Tribe Ammophilini
Genus *Ammophila* Kirby

14. *Ammophila azteca* Cameron.

Known biology. – Females prey on small larvae of sawflies and moths (recorded families – Geometridae, Gelechiidae, Sphingidae) and carry the prey in flight (Evans, 1970: 485). Evans (1965) presented a detailed study of the biology of this species.

Known distribution. – Wyoming: Jackson Hole (Evans, 1970).

Author's records. – NORTHWEST TERRITORIES. – III, ♂ 14 August 1967. V, ♀ 14 August 1967. VI, ♀ 29 July 1967; ♀ 12 August 1967. VII, ♀ 11 August 1967. IX, ♂ 1 August 1967. X, ♀ 11 July 1968; ♂, ♀ 17 July 1968; 3 ♂♂, ♀ 22 July 1967 (feeding on *Achillea* sp.); ♀ 25 July 1967; ♂, ♀ (*in copula*) 26 July 1967. XI, ♂, ♀ 2 August 1967; ♀ 8 August 1967. XII, ♂ 7 August 1967. XIII, 3 ♂♂, 2 ♀♀ 6 August 1967; ♀ 7 August 1967. XIV, ♂ 26 July 1968; ♂, ♀ 8 August 1967. XV, ♀ 8 August 1967. YUKON TERRITORY. – B, ♀ 15 August 1968. E, 3 ♀♀ 10 August 1968. G, 3 ♀♀ 12 August 1968.

15. *Ammophila mediata* Cresson.

Known distribution. – Ontario to British Columbia, Michigan to Colorado (Muesebeck et al., 1951: 976). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 129).

Author's records. – NORTHWEST TERRITORIES. – I, 2 ♀♀ 15 August 1967. IV, ♀ 28 July 1967. X, ♂, ♀ 21 July 1967. XIII, ♀ 30 July 1968. XIV, ♂ 26 July 1968; ♀ 8 August 1967. YUKON TERRITORY. – B, ♀ 15 August 1968. C, ♀ 9 August 1968.

16. *Ammophila strenua* Cresson.

Known distribution. – Western United States (Muesebeck et al., 1951: 977). Wyoming: Jackson Hole (Evans, 1970).

Author's records. – NORTHWEST TERRITORIES. – X, ♂ 21 July 1967.

Genus *Podalonia* Spinola

17. *Podalonia luctuosa* (F. Smith).

Known distribution. – Canada, United States – western and northern tier of states to Maine (Muesebeck et al., 1951: 977). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 128).

Author's records. – NORTHWEST TERRITORIES. – II, ♂ 14 August 1967. III, ♂ 14 August 1967. YUKON TERRITORY. – McGregor Creek, ♂ 10 August 1968.

18. *Podalonia robusta* (Cr.)

Known biology. – Prey: noctuid larva (Krombein et al., 1967: 404; *see also* Evans, 1963: 237).

Known distribution. – Canada; United States – western and northern tier of states to Maine (Muesebeck et al., 1951: 978). Alberta (Strickland, 1947: 128).

Author's records. – NORTHWEST TERRITORIES. – VI, ♀ 29 July 1967. IX, ♂ 1 August 1967. X, 6 ♂♂, ♀ 11 July 1968; ♀ 17 July 1968; ♂, ♀ 22 July 1967; 3 ♀♀ 25 July 1967; ♂, ♀ (*in copula*), ♀ 31 July 1967. XII, ♂, ♀ 29 July 1968; ♂ 7 August 1967. XIV, ♀ 8 August 1968. YUKON TERRITORY. – B, 2 ♀♀ (feeding on flowers and hunting(?) on the ground, respectively) 15 August 1968.

Also seen (but not captured): an entirely black specimen of (?) *Podalonia* sp. (XII).

Subfamily Nyssoninae
Tribe Alyssonini
Genus *Alysson* Panzer

19. *Alysson triangulifer* Provancher.
Author's records. – NORTHWEST TERRITORIES. – IX, ♀ 1 August 1967 (investigating leaves, in shrubs).

Tribe Nyssonini
Genus *Nysson* Latreille

Known biology. – Larvae of this genus are inquilinous in the nests of other sphecid wasps and bees (Muesebeck et al., 1951).

20. *Nysson lateralis* Packard.
Known distribution. – Chiefly Transition zone east of Rockies (Muesebeck et al., 1951: 983).
Author's records. – NORTHWEST TERRITORIES. – VII, ♀ 11 August 1967. IX, 2 ♀♀ 1 August 1967. X, ♀ 26 July 1967. XI, 2 ♀♀ 8 August 1967. XIII, ♀ 6 August 1967.

21. *Nysson subtilis* W. Fox.
Known biology. – Adults found along trail in open areas (Krombein, 1952a: 181).
Known distribution. – Pennsylvania, Illinois (Muesebeck et al., 1951: 983).
Author's records. – NORTHWEST TERRITORIES. – X, ♀ 22 July 1967; ♀ 25 July 1967; ♂, ♀ 31 July 1967. XI, ♀ 2 August 1967.

Tribe Gorytini
Genus *Lestiphorus* Lepeletier

22. *Lestiphorus cockerelli* (Rohwer).
Known distribution. – Eastern United States, northern tier west to Colorado (Muesebeck et al., 1951: 988).
Author's records. – NORTHWEST TERRITORIES. – X, ♀ 31 July 1967.

Genus *Gorytes* Latreille

23. *Gorytes albosignatus* W. Fox.
Known distribution. – Western United States, North Dakota to Montana, south to Nebraska (Muesebeck et al., 1951: 991). Wyoming: Jackson Hole (Evans, 1970: 494). Alberta (Strickland, 1947: 126).
Author's records. – NORTHWEST TERRITORIES. – X, ♀ 17 July 1968 (digging in sand hill).

Subfamily Philanthinae
Tribe Cercerini
Genus *Cerceris* Latreille

24. *Cerceris nigrescens nigrescens* F. Smith.
Known biology. – Females nest in the ground, and prey on weevils of the following

taxa: *Hyperodes delumbis* (Gyllenhal); *Sitona hispidula* (Fabricius); *Gymnaetron* sp.; *Gymnaetron antirrhini* (Paykull) (Evans, 1970: 501; Muesebeck et al., 1951: 1009; Scullen and Wold, 1969: 212). Scullen (1965: 494-495) lists the names of the plant species visited by adults of *C. nigrescens*.

Known distribution. – This is the most widely distributed species of *Cerceris* in North America, ranging from New England and adjacent southeastern Canada westward to the Pacific coast, northward to Alaska and south to Nevada and North Carolina (Muesebeck et al., 1951: 1009; Scullen, 1965: 492; Scullen and Wold, 1969: 212). Alberta (Strickland, 1947: 130).

Author's records. – NORTHWEST TERRITORIES. – I, ♀ 15 August 1967. VII, 2 ♀♀ 11 August 1967. IX, ♂, ♀ 1 August 1967. X, ♂ 11 July 1968; 3 ♂♂, 2 ♀♀ 22 July 1967; ♂, ♀ 25 July 1967; ♀ 31 July 1967. XI, 3 ♀♀ 2 August 1967; ♀ 8 August 1967. XII, ♂ 4 August 1967. XIII, ♀ 30 July 1968; ♀ 6 August 1967. XIV, ♂ 26 July 1968; 2 ♀♀ 8 August 1967. YUKON TERRITORY. – E, ♂, 3 ♀♀ 10 August 1968.

Subfamily Crabroninae
Tribe Crabronini
Genus *Crabro* Fabricius

Known biology. – Females nest principally in soil, though occasionally in rotten wood and prey on flies (Muesebeck et al., 1951: 1015). Kurczewski and Acciavatti (1968) review nesting behavior of the Nearctic species.

25. *Crabro latipes* F. Smith.

Known biology. – A detailed study of nesting behavior is provided by Kurczewski, Burdick and Gaumer (1969). Nests are in open areas with sparse vegetation. Prey consists of a wide variety of average-size flies of rather stocky build, such as individuals of *Musca domestica* Linnaeus (Muesebeck et al., 1951: 1017) and *Musca autumnalis* DeGeer (Kurczewski and Harris, 1968).

Known distribution. – Transcontinental in the north, in Canada, Alaska and the Canadian and Transition zones of conterminous United States (Muesebeck et al., 1951: 1017). Alberta (Strickland, 1947: 127).

Author's records. – NORTHWEST TERRITORIES. – VI, ♂, 4 ♀♀ 29 July 1967. VII, ♂ 11 August 1967. X, ♂, ♀ 11 July 1968; ♂ 17 July 1968 (on leaves of willows? pouncing on other males of apparently the same species); ♀ 21 July 1967 (investigating holes in the ground); ♀ 22 July 1967; ♀ 25 July 1967; ♂ 26 July 1967; 2 ♂♂, ♀ 31 July 1967. XI, 3 ♂♂ 2 August 1967. XII, ♀ 7 August 1967 (on leaves, shrub). XIII, ♂ 6 August 1967 (on leaves, shrub); 4 ♂♂ 7 August 1967. XIV, 2 ♂♂ 8 August 1967 (on leaves of small *Alnus* ?). YUKON TERRITORY. – G, ♂ 12 August 1968.

26. *Crabro* sp.

Author's records. – NORTHWEST TERRITORIES. – XIII, ♀ 30 July 1968.

Genus *Crossocerus* Lepeletier and Brullé

Known biology. – Females usually nest in soil, occasionally in cracks in walls or in abandoned beetle burrows in wood. Prey consists of small flies (Muesebeck et al., 1951: 1020).

27. *Crossocerus* species.

Author's records. – NORTHWEST TERRITORIES. – IX, 31 July 1967. X, ♂, 3 ♀♀ 31 July 1967. XIV, ♀ 8 August 1967.

Genus *Ectemnius* Dahlbom

28. *Ectemnius arcuatus* Say.

Known biology. – Females nest in logs. They prey on flies of the species *Musca domestica* L. (Muesebeck et al., 1951: 1026; under the name *Hypocrabro chrysargirus* (Lepeletier and Brullé)).

Known distribution. – Transcontinental in Transition and Austral zones (Muesebeck et al., 1951: 1026; under the name *Hypocrabro chrysargirus* (Lepeletier and Brullé)).

Author's records. – NORTHWEST TERRITORIES. – X, ♀ 17 July 1968 (feeding on *Epilobium* sp. flowers).

29. *Ectemnius dives* (Lepeletier and Brullé).

Known biology. – Females nest in logs, timber and stems. Prey consists of muscoid Diptera (Muesebeck et al., 1951: 1027). Kurczewski and Kurczewski (1963: 148) observed males on flowers of *Daucus carota* and *Achillea millefolium*.

Known distribution. – Holarctic. Nearctic Region: transcontinental in Canadian and Transition zones of Canada and United States (Muesebeck et al., 1951: 1027). Alberta (Strickland, 1947: 127). Palaearctic Region: Germany, Austria, Switzerland and Morocco (Leclercq, 1949: 11).

Author's records. – NORTHWEST TERRITORIES. – X, 2 ♂♂ 11 July 1968; ♂ 25 July 1967; 2 ♂♂ 26 July 1967; 3 ♀♀ 31 July 1967.

30. *Ectemnius lapidarius* (Panzer).

Known biology. – Adults are in open woods and at the edge of woods, on flowers of *Solidago* sp., and of *Daucus carota* (Kurczewski and Kurczewski, 1963: 148).

Known distribution. – Holarctic. Nearctic Region: Pennsylvania (Kurczewski and Kurczewski, 1963: 148). Wyoming: Jackson Hole (Evans, 1970: 492). Alberta (Strickland, 1947: 127). Palaearctic Region: Finland, Germany and Austria (Leclercq, 1949).

Author's records. – YUKON TERRITORY. – Lake Labarge, ♀ 6 August 1968. G, ♀ 12 August 1968.

31. *Ectemnius nigrifrons* (Cresson).

Known biology. – Recorded as prey is the fly species *Syrphus ribesii* (Linnaeus) by Muesebeck et al., (1951: 1024; under the name *Clytochrysus nigrifrons*).

Known distribution. – Holarctic. Nearctic Region: transcontinental, chiefly in Transition zone (Muesebeck et al., 1951: 1024; under the name *Clytochrysus nigrifrons*). Alberta (Strickland, 1947: 127). Palaearctic Region: Switzerland (Leclercq, 1949).

Author's records. – NORTHWEST TERRITORIES. – II, ♀ 14 August 1967. V, ♀ 14 August 1967. IX, ♂, 2 ♀♀ 1 August 1967. X, ♀ 11 July 1968; 2 ♂♂ 17 July 1968. XIII, ♀ 7 August 1967. YUKON TERRITORY. – C, 2 ♀♀ 9 August 1968 (stalking behavior: react to slightest movements by orienting responses; also intense visual scanning; hunting behavior?); 2 ♀♀ 10 August 1968 (same remark, concerning hunting behavior?). E, ♀ 10 August 1968. G, 2 ♀♀ 12 August 1968.

32. *Ectemnius trifasciatus* (Say).

Known distribution. – Transition zone of Canada and United States, east of the

Cascade and Sierra Nevada ranges (Leclercq, 1949: 11; Muesebeck et al., 1951: 1027, under the name *Hypocrabro trifasciatus*). Alberta (Strickland, 1947: 127).

Author's records. – NORTHWEST TERRITORIES. – III, ♀ 14 August 1967. X, 2 ♀♀ (investigating the ground) 17 July 1968. XIV, ♀ 26 July 1968.

33. *Ectemnius* species.

Author's records. – NORTHWEST TERRITORIES. – X, ♀ 31 July 1967. XIII, ♀ 7 August 1967.

Genus *Lestica* Billberg

34. *Lestica producticollis* (Packard).

Known biology. – One ♀ found in woods (Krombein, 1952b: 338).

Known distribution. – Transcontinental; in Canada and United States in Transition and Upper Austral zones (Muesebeck et al., 1951: 1028; under the name *Solenius producticollis* (Packard)). Alberta (Strickland, 1947: 127).

Author's records. – NORTHWEST TERRITORIES. – X, ♂ 9 August 1967.

Tribe Oxybelini
Genus *Oxybelus* Latreille

35. *Oxybelus uniglumis quadrinotatus* Say.

Known biology. – Females dig nests in light, friable sand (Evans, 1970: 493). Prey consists of flies of the following taxa: *Symphoromyia* sp.; *Musca domestica* Linnaeus; *Ophyra leucostoma* Wiedemann; *Sarcophaga rapax* Walker; *Hylemya cilicrura* (Rondani), and other muscids, and anthomyiids (Evans, 1970: 493; Muesebeck et al., 1951: 1033, under the name *Oxybelus quadrinotatus*). Evans (1962: 477) presents a detailed study of prey-carrying behavior.

Known distribution. – Generally distributed throughout the United States and southern Canada (Muesebeck et al., 1951: 1033; under the name *Oxybelus quadrinotatus*).

Author's records. – NORTHWEST TERRITORIES. – V, ♀ 14 August 1967. X, ♀ 11 July 1968 (digging in sand); ♀ 25 July 1967 (digging in sand); ♂, ♀ 26 July 1967; 2 ♀♀ 31 July 1967. XI, ♀ 2 August 1967. XIV, ♂ 26 July 1968.

DISTRIBUTION PATTERNS OF THE SUBARCTIC SPHECID FAUNA AND FACTORS AFFECTING ITS DIVERSITY

The samples of sphecid wasps from the Yukon and Northwest Territories here discussed indicate that the fauna is impoverished in terms of number of taxa compared with that of more southern climates. These subarctic samples comprise 35 species in 21 genera or subgenera. In contrast, at Jackson Hole, Wyoming (44°N., 5750 feet above sea level at Moran) there are 94 species in 42 genera or subgenera (Evans, 1970), and in Alberta 160 species in 53 genera or subgenera (Strickland, 1947). The latter area is much more extensive and was sampled over a longer period of time than were the subarctic areas described here, so part of the difference in diversity between the two must be the result of these factors.

That the number of species included in most genera is higher farther south than in subarctic areas is illustrated by the following examples. Following each generic name is, first, the number of species from Jackson Hole, Wyoming, and second, the number of species in the subarctic samples: *Podalonia*, 6 vs. 2; *Ammophila*, 9 vs. 3; *Tachysphex*, 5 vs. 3; *Crabro*,

4 vs. 2; *Ectemnius*, 9 vs. 6.

Although these comparisons demonstrate faunal impoverishment over a wide range of latitudes, this phenomenon is not so well marked within the limits of the study area, except perhaps in the Yukon, where the study area extended almost 2° of latitude farther north than in the Northwest Territories study area (see Table 1; localities are listed from left to right, in order of increasing latitude for each study area). A more conclusive comparison should, however, involve both standardization of the conditions of sampling in time, space, and season; and rating of the localities in terms of vegetation, local climate, and soil conditions.

Comparison between rows rather than columns is probably more reliable: it gives an indication of how common and/or widespread each species is, assuming that sampling biases are equally distributed over species or nearly so.

Some groups of sphecids, represented by an abundance of species southward have few species in subarctic regions. For example, there are few Sphecinae in the sample. Of four tribes in this subfamily, only one, the Ammophilini, is represented in the study area. One ammophiline, *Ammophila azteca*, was one of the commonest and most widespread sphecids encountered. Wasps of this genus are also at high latitudes and altitudes in Europe. Another subfamily with many taxa farther south is the Nyssoninae. Of six tribes, only three are represented in the subarctic study areas.

In contrast, the subfamily Crabroninae is well represented, both in numbers of species and in numbers of individuals in these samples (10 species from a total of 35 sphecid wasps, or almost a third; and 39 species from a total of 160 Albertan species, or a quarter). Some subarctic crabronines are Holarctic.

Other wasp groups from the study areas with northern affinities are *Dryudella* (subfamily Astatinae), some Gorytini (species 22 and 23), and some Pemphredoninae (species 10 and 13). The last-named subfamily is represented by six species in my samples. Like crabronines, pemphredonines are very abundant and widely distributed over the study areas.

Some of the species represented in the samples are widely distributed on the North American continent, particularly latitudinally. Some are transcontinental such as *Astata nubecula*, (ranging southward to New Mexico and California) and *Miscophus americanus* (ranging southward to Florida and Texas). Wasps of the tribe Tachytini are well represented in temperate as well as tropical areas of the world. Many are wide-ranging on this continent, for example, *Tachysphex quebecensis* and *T. terminatus* (species 6 and 7). Another species of the genus, *T. aethiops*, is, however, restricted to relatively high latitudes or altitudes. *Cerceris nigrescens* and *Oxybelus uniglumis* also range widely. Among pemphredonines, *Mimesa clypeata* (species 10) and *Pemphredon bipartior* (species 12) are wide-ranging, as are a number of crabronines (species 25, 28, 30, 31, 32 and 34).

Routes of dispersal are probably river valleys for southern-based species, and the north-south trending mountain systems for northern-based species.

In conclusion, the subarctic sphecid fauna comprises elements derived from cold-adapted groups as well as wide-ranging species probably derived from warm-adapted groups. Although diversity is limited, the fauna is nonetheless quite varied for high latitudes. What makes it possible for these insects to live so far north? We do not know, but factors can be suggested, in general terms. Local conditions of climate, soil, vegetation and microclimates are likely important (Corbet, 1969; Geiger, 1965; Uvarov, 1931). An important behavioral adaptation is probably that of basking, which enables a flying insect to accumulate sufficient solar energy even when the air temperature is quite low (Baker and Hurd, 1968; Clench, 1966; Digby, 1965; Downes, 1964; Hocking and Sharplin, 1965; Kevan, 1970; Kevan and Shorthouse, 1970; Monroe, 1956; Parry, 1951; Richards, 1970). Physiological

adaptations to the cold which make possible survival through the winter are also probably important (Aoki, 1956; Asahina, 1959, 1966, 1969; Dubach et al., 1959; Losina-Losinsky, 1962; Salt, 1961; Scholander et al., 1953; Smith, 1961; Sømme, 1964; Tanno, 1964; Ushatinskaya, 1957).

The next phase of study of the subarctic sphecid fauna should aim at elucidating these factors.

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REFERENCES

Aoki, K. 1956. The undercooling point and frost resistance in the prepupa of a ruby-tailed wasp, *Crysis (Pentacrysis) shanghaiensis* [in Japanese]. Low Temp. Sci. Ser. B. 14:121-124.

Asahina, E. 1959. Cold hardiness in overwintering insects [in Japanese], p. 99-113. *In* M. Fukaya, M. Harizuka and K. Takewaki [ed.] Recent advances in experimental morphology. Yokendo: Tokyo.

Asahina, E. 1966. Freezing and frost resistance in insects, p. 451-486. *In* H. T. Meryman [ed.] Cryobiology. Acad. Press, London.

Asahina, E. 1969. Frost resistance in insects, p. 1-49. *In* J. L. Beament, J. E. Treherne and V. B. Wigglesworth [ed.] Advances in insect physiology. Acad. Press, London.

Baker, H. G. and P. D. Hurd. 1968. Interfloral ecology. A. Rev. Ent. 13:385-414.

Clench, H. K. 1966. Behavioral thermoregulation in butterflies. Ecology 47:1021-1034.

Corbet, P. S. 1969. Terrestrial microclimate: ameliorations at high latitudes. Science 166: 865-866.

Digby, P. S. B. 1955. Factors affecting temperature excess of insects in sunshine. J. exp. Biol. 32:279-298.

Downes, J. A. 1964. Arctic insects and their environment. Can. Ent. 96:279-307.

Dubach, P., F. Smith, D. Pratt and C. M. Stewart. 1959. Possible role of glycerol in the winter-hardiness of insects. Nature, Lond. 184:288-289.

Evans, H. E. 1957. Ethological studies on digger wasps of the genus *Astata* (Hymenoptera, Sphecidae). J. N. Y. ent. Soc. 65:159-185.

Evans, H. E. 1962. The evolution of prey-carrying mechanisms in wasps. Evolution. Lancaster, Pa. 16(4):468-483.

Evans, H. E. 1963. Notes on the prey and nesting behavior of some solitary wasps of Jackson Hole, Wyoming. Ent. News 74(9):233-239.

Evans, H. E. 1965. Simultaneous care of more than one nest by *Ammophila azteca* Cameron (Hymenoptera, Sphecidae). Psyche, Camb. 72:8-23.

Evans, H. E. 1970. Ecological-behavioral studies of wasps of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. 140(7):451-511.

Geiger, R. 1965. The climate near the ground. Harvard Univ. Press, Cambridge, Mass. xiv + 611 p.

Hartman, F. 1905. Observations on the habits of some solitary wasps of Texas. Bull. Univ. Texas, No. 65. 72 p., 4 plates.

Hocking, B. and C. D. Sharplin. 1965. Flower basking by Arctic insects. Nature, Lond. 206(4980):215.

Kevan, P. G. 1970. High Arctic insect flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N. W. T., Canada. Unpubl. Ph.D. thesis, Univ. Alberta. 399 p.

Kevan, P. G. and J. D. Shorthouse. 1970. Behavioral thermoregulation by High Arctic butterflies. Arctic 23(4):268-279.

Krombein, K. V. 1952a. Preliminary annotated list of the wasps of Lost River State Park, West Virginia, with descriptions of new species and biological notes. Proc. ent. Soc. Wash. 54(4):175-184.

Krombein, K. V. 1952b. Biological and taxonomic observations on the wasps on a coastal area of North Carolina (Hymenoptera: Aculeata). Wasmann J. Biol. 10(3):257-341.

Krombein, K. V. 1967. Trap-nesting wasps and bees: Life histories, nests, and associates. Washington, D. C.: Smithsonian Press, 570 p.

Krombein, K. V. et al. 1958. First Supplement to "Hymenoptera of America . . . " (see Muesebeck, C. F. W., below).

Krombein, K. V., B. D. Burks et al. 1967. Second Supplement to "Hymenoptera of America . . . " (see Muesebeck, C. V. W., below).

Kurczewski, F. E. 1966a. *Tachysphex terminatus* preying on Tettigoniidae – an unusual record (Hymenoptera: Sphecidae: Larrinae). J. Kans. ent. Soc. 39:317-322.

Kurczewski, F. E. 1966b. Comparative behavior of male digger wasps of the genus *Tachysphex* (Hymenoptera: Sphecidae: Larrinae). J. Kans. ent. Soc. 39(3):436-453.

Kurczewski, F. E. 1969. Comparative ethology of female digger wasps in the genera *Miscophus* and *Nitelopterus* (Hymenoptera: Sphecidae, Larrinae). J. Kans. ent. Soc. 24(4): 470-509.

Kurczewski, F. E. and R. E. Acciavatti. 1968. A review of the nesting behaviors of the nearctic species of *Crabro*, including observations on *C. advenus* and *C. latipes* (Hymenoptera: Sphecidae). J. N. Y. ent. Soc. 76(3): 196-212.

Kurczewski, F. E. and B. J. Harris. 1968. The relative abundance of two digger wasps, *Oxybelus bipunctatus* and *Tachysphex terminatus*, and their associates, in a sand pit in central New York. J. N. Y. ent. Soc. 76(2):81-83.

Kurczewski, F. E. and E. J. Kurczewski. 1963. An annotated list of digger wasps from Presque Isle State Park, Pennsylvania. Proc. ent. Soc. Wash. 65(2):141-149.

Kurczewski, F. E., N. A. Burdick and G. C. Gaumer. 1969. Additional observations on the nesting behaviors of *Crabro advenus* Smith and *C. latipes* Smith (Hymenoptera: Sphecidae). J. N. Y. ent. Soc. 77(3):152-170.

Leclercq, J. 1949. Contribution à l'étude des Crabroninae (Hym. Sphecidae) de l'Hémisphère Nord. Bull. Instit. Roy. Belg. 25(16):1-18.

Losina-Losinsky, L. K. 1962. Survival of insect at super-low temperatures. Dokl. Akad.

Nauk. SSSR 147:1247-1249.
Monroe, E. 1956. Canada as an environment for insect life. Can. Ent. 88:372-476.
Muesebeck, C. F. W., K. V. Krombein, H. K. Townes et al. 1951. Hymenoptera of America north of Mexico – Synoptic Catalog. U. S. Dept. Agric. (Agriculture Monograph No. 2), Washington, 1420 p.
Parry, D. A. 1951. Factors determining the temperature of terrestrial arthropods in sunlight. J. exp. Biol. 28:445-462.
Richards, K. W. 1970. Biological studies of Arctic bumblebees. Unpubl. M.Sc. thesis, Univ. Alberta. 165 p.
Salt, R. W. 1961. Principles of insect cold-hardiness. A. Rev. Ent. 6:55-74.
Scholander, P. F., W. Flagg, R. J. Hock and L. Irving. 1953. Studies on the physiology of frozen plants and animals in the Arctic. J. cell. comp. Physiol. 42, Suppl. 1:1-56.
Scullen, H. A. 1965. Review of the genus *Cerceris* in America North of Mexico (Hymenoptera: Sphecidae). Proc. U. S. National Mus. 116:333-548.
Scullen, H. A. and J. L. Wold. 1969. Biology of wasps of the tribe Cercerini, with a list of the Coleoptera used as prey. Ann. ent. Soc. Am. 62(1):209-214.
Smith, A. V. 1961. Biological effects of freezing and super-cooling. Edward Arnold Ltd., London, 462 p.
Sømme, L. 1964. Effects of glycerol on cold-hardiness in insects. Can. J. Zool. 42:87-101.
Spooner, G. M. 1948. The British species of psenine wasps. Trans. R. ent. Soc. London, 99:129-172.
Steiner, A. L. 1970. Solitary wasps from subarctic North America – I. Pompilidae from the Northwest Territories and Yukon, Canada. Quaest. ent. 6:223-244.
Strickland, E. H. 1947. An annotated list of the wasps of Alberta. Can. Ent. 79:121-130.
Tanno, K. 1964. High sugar levels in the solitary bee, *Ceratina* [in Japanese, English summary]. Low Temp. Sci. Ser. B. 22:51-57.
Ushatinskaya, R. S. 1957. Principles of cold resistance in insects [in Russian]. Acad. Sci. USSR Press, Moscow. 314 p.
Uvarov, B. P. 1931. Insects and climate. Trans. R. ent. Soc. Lond. 79:1-247.
Williams, F. X. 1946. Two new species of Astatinae, with notes on the habits of the group. Proc. Hawaiian ent. Soc. 12(3):641-650.